QUADRUPLE, TRIPLE, DOUBLE, AND SIMPLE PAPPI IN THE GOLDENASTERS, SUBTRIBE CHRYSOPSIDINAE (ASTERACEAE: ASTEREAE)

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ABSTRACT

Pappus variation in eight genera, 58 species, and 94 taxa of the Chrysopsidinae was examined; quadruple, triple, double and sometimes simple pappi were found with variation in the size, shape and numbers of short outer scales/bristles and mid to long barbellate bristles. In the genera with a higher chromosome base number ($x = 9$)—*Heterotheca*, *Noticastrum*, *Pityopsis*, and probably *Tomentaurum*—pappus elements are more numerous and in a greater number of series. This is interpreted as the primitive condition, similar to, but with less clavate inner bristles, than found in *Doellingeria* and *Eucephalus*, the basal genera in the North American Clade of the Astereae. All four genera have a quadruple pappus consisting of four, sometimes intergrading, series: a short secondary outer series of scales or scaly bristles; a secondary inner series of mid-length tapered bristles; a primary outer series of tapering bristles 80–95% the length of the inner series; and a primary inner series of usually weakly clavate bristles. Both ray and disc florets have a similar arrangement, except for the epappose ray fruits of *H.* sect. *Heterotheca*. In some species, the four series are distinct and in others they grade into each other. In *Croptilon*, the number of pappus series decreases with the dysploid reduction from $x = 7$ to $x = 4$. In the lower base number genera *Bradburia*, *Chrysopsis*, and *Osbertia*, a reduction in the number of series was observed, with quadruple, triple, double and sometimes simple pappi occurring. In *Chrysopsis*, the secondary outer series is well developed, but the secondary inner series is absent or reduced to a few bristles. In *Osbertia*, the pappus appears simple or includes a second series of 1–2 short bristles; all the long bristles are tapering or at best only very weakly clavate. In small sample per species, the number of bristles per fruit ranged from 20–125: *Noticastrum*, 46–125 averaging 87 bristles; *Tomentaurum*, 80–85; *Heterotheca*, 23–80 averaging 43 bristles; *Pityopsis*, 25–46, averaging 37; *Bradburia*, ray florets, 30–36, discs 0–5; *Chrysopsis* and *Croptilon*, 18–36 averaging 28; *Osbertia*, 20–35, averaging 27. The fruits with lower numbers of bristles had 0–few mid-length secondary inner series bristles.

RESUMEN

Se examinó la variación el vilano en ocho géneros, 58 especies, y 94 taxa de Chrysopsidinae; se encontraron vilanos cuádruples, triples, dobles y a veces simples con variación en el tamaño, forma y números de las escamas cortas externas y las sedas barbeladas medias a largas. En los géneros con un número cromosomático básico más alto ($x = 9$)—*Heterotheca*, *Noticastrum*, *Pityopsis*, y probablemente *Tomentaurum*—los elementos del vilano son más numerosos y están en mayor número de series. Esto se interpreta como una condición primitiva, similar pero con menos sedas interiores clavadas de las que se encuentran en *Doellingeria* y *Eucephalus*, los géneros basales del clado norteamericano de las Astereae. Los cuatro géneros tienen un vilano cuádruple que consta de cuatro series, a veces intergradadas: una serie corta secundaria de escamas o sedas escamosas; una serie secundaria interna

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de sedas afiladas de longitud media; una serie primaria externa de sedas afiladas del 80–95% de la longitud de la serie interna; y una serie primaria interna de sedas normalmente clavadas. Tanto las flores radiadas como las del disco tienen una ordenación similar, excepto los frutos sin vilano de *H.* sect. *Heterotheca*. El algunas especies, las cuatro series son distintas y en otras se intergradan entre ellas. En *Croptilon*, el número de series del vilano decrece con la reducción disploide de x =7 a x = 4. En los géneros con número base inferior *Bradburia*, *Chrysopsis*, y *Osbertia*, se ha observado una reducción en el número de series, con vilanos cuádruples, triples, dobles y a veces simples. En *Chrysopsis*, la serie secundaria externa está bien desarrollada, pero la serie secundaria interna está ausente o reducida a unas pocas sedas. En *Osbertia*, El vilano es simple o incluye una segunda serie de 1–2 sedas cortas; todas las sedas largas son afiladas o como mucho sólo débilmente clavadas. En una pequeña muestra por especie, el número de sedas por fruto varió entre 20–125: *Noticastrum*, 46–125 con una media de 87 sedas; *Tomentaurum*, 80–85; *Heterotheca*, 23–80 con una media de 43 sedas; *Pityopsis*, 25–46, con una media de 37; *Bradburia*, flores radiadas, 30–36, del disco 0–5; *Chrysopsis* and *Croptilon*, 18–36 con una media de 28; *Osbertia*, 20–35, con una media de 27. Los frutos con menor número de sedas tuvieron 0–few en la serie secundaria interna de longitud media.

INTRODUCTION

Goldenaster genera in the subtribe Chrysopsidinae Nesom (Asteraceae: Astereae) have long been reported to have a double pappus consisting of a short outer whorl of narrow to broad scales or linear bristles (e.g., Gray 1884; Fernald 1950; Cronquist 1968, 1980; Semple 1981, 1996; Semple & Bowers 1985; Semple et al. 1988). Nesom (1994a) in his protologue to subtribe Chrysopsidinae described the pappus as "2–3(–4)-seriate, persistent, the inner of 1–2 series of generally flattened bristles, outer of much shorter setae, bristles, or scales," but did not elaborate as to the number of series in each genus. Nesom (2000) described the pappi of the North American genera as follows: *Croptilon*, "pappus a single series of persistent, thick and rigid, equal-length, tawny to reddish-brown capillary bristles"; *Chrysopsis* (including *Bradburia*), "pappus in 2 series, the outer very short bristles, the inner of long capillary bristles"; *Heterotheca*, "pappus of tawny to whitish barbellate bristles somewhat uneven in length, with a shorter, outer series of lanceolate scales or bristle-like squamellae" and noted the epappose to few bristled ray floret cypselae of sect. *Heterotheca*; *Osbertia*, "pappus uniseriate, with numerous, nearly non-barbellate bristles, a short, outer series commonly present in *O. chihuahuana*"; *Pityopsis*, "pappus 2-seriate, the inner of barbellate bristles, the outer of much shorter setiform bristles or setae"; and *Tomentaurum*, "pappus of 45–60 white, barbellate bristles in several series, with a few inconspicuous setae or very slightly widened bristles, 0.5–1.5 mm long." Nesom (1994a, 2000) did not indicate which taxa had the flattened inner bristles. *Noticastrum* is native to South America and was not discussed in Nesom (2000). Zardini (1985) monographed the genus and described the pappus as being in two series, the external morphologically similar to the internal but of short bristles, normally straw-colored or reddish [five species] to purplish in *N. diffusum* and the bristles barbellate especially distally. Zardini also noted that the cypsela body was glandular in some taxa.

Many other North American Astereae have been reported to have a simple pappus. Some asters often treated in *Aster* sensu lato have been reported to have a "double" pappus (*Eucephalus* Nutt., *Sericocarpus* Nees: Gray 1884; Cronquist 1955) or a "triple" pappus (*Doellingeria* Nees: Cronquist 1968, 1980; Nesom 1994a,b; Semple et al. 2002). The "triple" pappus reportedly had two inner whorls, the outer slightly shorter and tapering and the inner bristles clavate. However, Hood and Semple (2003) demonstrated that nearly all species of goldenrods, which had been reported to have a simple pappus, in fact had a double pappus with two primary series of long bristles (the outer shorter and tapering, the inner clavate) and at least some species had a secondary outer series of a few very short bristles, i.e. *Solidago* has a double or triple pappus. Semple and Hood (2005) demonstrated that many North American aster genera have a double, triple, or quadruple pappus and concluded that the likely primitive pappus of the North American Astereae consists of four series: the primary inner series of long, clavate (flattened) bristles, a slightly shorter primary outer series of long tapering bristles, a secondary inner series of tapering bristles 40–80% the length of the primary inner bristles, and a secondary outer series of short bristles or narrow to broad squamellae usually only 10–15% the length of the inner primary bristles. Hood and Semple (2003) proposed a terminology for a triple pappus, i.e. secondary outer whorl, primary outer whorl, and primary inner whorl bristles, which Semple and Hood (2005) modified to cover the discovery of a fourth series of bristles found in asters but not seen in goldenrods. They also noted that "series" was a more accurate label than "whorl" based on observations of both North American and Old World aster genera. They concluded that due to the subtlety of the differences between the longer bristle series in many species, it would be practical to treat the pappus of *Symphyotrichum* as "appearing simple" in keys to identification. The details of the "double pappus" of the Chrysopsidinae were re-examined in light of the recent discoveries on pappus traits of goldenrods and asters and the results are presented in this paper.

MATERIALS AND METHODS

A preliminary survey was undertaken to examine the pappus of one or two specimens of representative species of the genera of the Chrysopsidinae sensu Nesom (2000). Subsequently, a more detailed survey was conducted involving eight genera, 58 species, and 94 taxa of subtribe Chrysopsidinae listed in Table 1. Observations were made using a dissecting scope (10–70×) or a compound light microscope (20–400×). The degree of the clavateness of bristle tips was determined using the 0–4 rankings described in detail in Hood and Semple (2003). At least five different fruits from each species were observed under the dissecting microscope at a maximum of 70×; in some cases many fruits from many individuals were examined to investigate the frequency of variation. The

majority of observations were made on specimens in the WAT Herbarium; additional specimens on loan from MEXU, MO, OS, SD, TEX-LL and UC (Holmgren et al. 1990) were also examined. In addition to the several methods used in evaluating pappus features listed by Hood and Semple (2003), assessment of the characteristics of the short secondary outer scales or bristles was also systematically undertaken with three traits recorded. The large difference in numbers of pappus bristles per fruit noted in the preliminary survey and the literature led to recording a rough estimate of bristle number for each taxon by counting the number of bristles on three to five representative fruits per taxon. These were compared to counts of numbers of bristles in (Smith 1965; Nesom 1991b; Semple & Bowers 1995; Semple 1996). Thus, Table 1 has eight columns of observational data plus a column for additional comments, while only four were reported by Hood and Semple (2003) and five in Semple and Hood (2005).

Observations on the compound microscope were made from both unmounted fruits and from slides prepared following Semple and Hood (2005). For each species, usually two to three disc floret cypselae with or without corollas were mounted in Cytoseal-60™ mounting medium under a cover slip; immature ray floret fruits were also often mounted on the same slide for comparison. Observations at 20–400× on the compound microscope were made similarly to the observations under the dissecting scope at 30–70×. Observations made on the two kinds of scopes were compared and any discrepancies were resolved by re-examining specimens.

Digital photomicrographs were taken using a Nikon CoolPix 990 camera manually held against the ocular lens of either the dissecting or compound microscope. Pictures were taken of specimens under the compound light microscope with either below stage or above stage lighting. Scanning Electron Microscope (SEM) photomicrographs were made using Kodak FX or Ilford Pan F Plus film commercially developed and subsequently digitized by scanning the negatives. Final digital illustrations were made using CorelDraw 12® from digital images edited with Corel PhotoPaint12® (Corel Corp.). In some illustrations, the contrast was manipulated to increase the difference between pappus bristles and background for illustrative purposes; backgrounds were darkened considerably and sometimes bristles were lightened somewhat to correct for uneven lighting and exposure; the converse was done in bristle tip silhouette illustrations.

RESULTS AND DISCUSSION

The pappus of most species of the Chrysopsidinae consists of 3–4 series (Figs. 1–7) while a minority of taxa has a pappus of 1–2 series (Fig. 8). The quadruple pappus consists of the following series: 1) a well develop secondary outer series usually of many, short, linear-bristly to broad scales; 2) a secondary inner series of mid-length, tapering, non-clavate bristles that were generally 40–80% the length of the primary inner series (Figs. 1F, 1J, 2F, 2N, 4K, 5A, 5M, 6A); 3) a

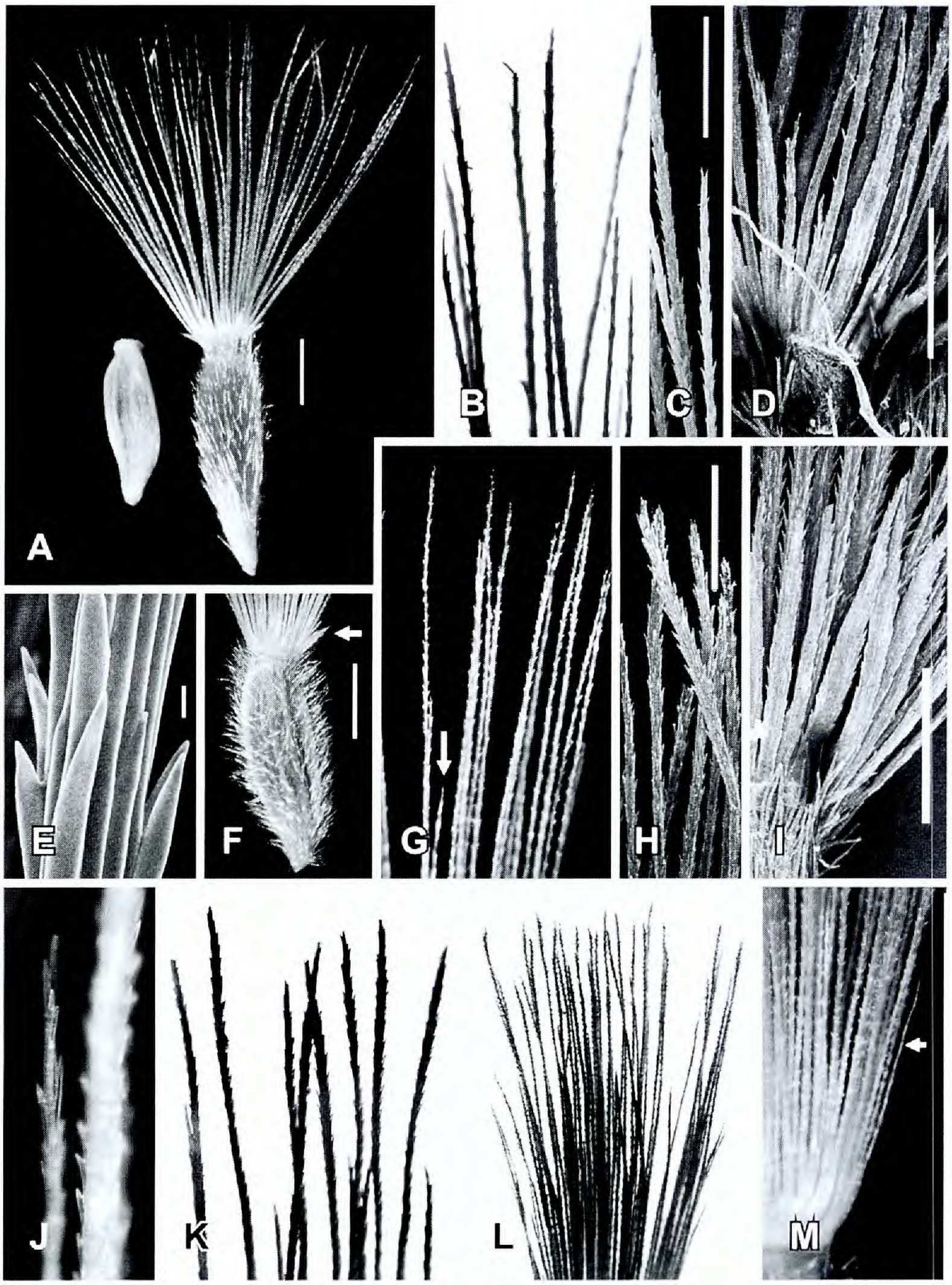

FIG. 1. Fruit and pappus traits of *Heterotheca*, disc fruits except A; scale bars = 1 mm in A and F, = 0.5 mm in C–D and H–I, and = 10 μm in E. **A–B.** *H. grandiflora* (*Semple & Semple 5575* WAT). **A.** Mature epappose ray and pappose disc fruit. **B.** Silhouette of tips of primary inner (long) and outer bristles. **C–E.** *H. inuloides* var. *viridis* (*Canne & Woodland 1928* WAT), SEMs. **C.** Tip of mid length secondary inner bristle. **D.** Secondary outer series scales and overlapping bases of longer bristles. **E.** Detail of barbs on mid portion of inner series bristle. **F–G.** *H. mexicana* (*Teppner s.n.* WAT). **F.** Mature fruit body and secondary outer series bristles (arrow). **G.** Upper portion of secondary inner (arrow) and primary bristles. **H–I.** *H. sessiliflora* subsp. *bolanderioides* (*Semple & Chmielewski 8918a* WAT; SEMs). **H.** Weakly clavate tips of primary inner series bristles. **I.** Secondary outer series scales. **J.** *H. canescens* (*Harms 871* WAT), tip of mid length secondary inner bristle. **K.** *H. camporum* var. *camporum* (*Semple 9902* WAT), clavate tips of primary inner bristles and non-clavate tips of shorter primary outer bristles. **L–M.** *H. oregona* var. *compacta* (*Semple & Heard 5693* WAT). **L.** Silhouette of upper portion of mid length secondary inner bristles and long primary outer and inner bristles. **M.** Linear secondary outer bristle (arrow).

primary outer series of tapering bristles that were 85–95% the length of the primary inner series (Figs. 1B, 1I, 1J, 3D, 4D, 4G, 4K, 5G, 5K, 6KC, 7B, 7E, 7I, 7K, 8A, 8C); and 4) a primary inner series of very subtly to moderately clavate tipped bristles (Figs. 1B, 1I, 4D, 5B, 6D, 7E, 7J). A four-series pappus is plesiomorphic in the North American Clade (sensu Noyes & Rieseburg 1999) of the tribe Astereae (Semple & Hood 2005). *Heterotheca*, *Noticastrum*, and *Pityopsis*, with the plesiomorphic chromosomal base number of $x = 9$, has a quadruple pappus in all or most species, as does the monotypic *Tomentaurum*, whose chromosome number is not yet known but is hypothesized here to be $x = 9$ based on indument and fruit similarities with $x = 9$ *Noticastrum*.

In the genera with lower chromosomal base numbers, *Croptilon* (synonym: *Haplopappus* sect. *Isopappus*: Hall 1928), *Chrysopsis*, and *Bradburia*, the pappus is usually reduced to three pappus series or less but sometimes had 1–few bristles of one or both of the missing series. *Osbertia*, which also was included in *Haplopappus* by Hall (1928), has a vestigial secondary series and a possible biseriate primary series. Thus, in all genera of the Chrysopsidinae, some evidence was found for the presence of at least 2–3 pappus series and usually more.

A large range in pappus lengths and numbers of bristles was observed among genera and within some genera of Chrysopsidinae. The smallest fruits with the lowest numbers of bristles were seen in *Bradburia*, *Chrysopsis*, *Croptilon*, and *Osbertia*. These traits vary considerably in *Heterotheca* and *Pityopsis*. The majority of species of *Noticastrum* examined had the longest pappus bristles and the highest number of bristles observed. Pappus and fruit traits are discussed in detail below by genus with higher base number genera presented first. Data for all taxa examined are presented in Table 1.

***Heterotheca* ($x = 9$; all 24 species, all 48 taxa examined).**—Cypselae straw colored to brown, obconic, compressed laterally or not, those of ray florets often 3-angled, 1–4.3 mm long, sparsely to moderately strigose, dimorphic in sect. *Heterotheca* (Fig. 1A), ray florets usually lacking a pappus and glabrous, rarely pappose and intermediate; ribs 5–10, sometimes dark, resin filled; pappi quadruple or sometimes triple through loss of the secondary inner series, series often intergrading; 23–80 mid to long bristles, averaging about 43 per fruit for the genus, barbs usually evenly arranged around the round shaft for most or all the length of the bristle; secondary outer series obvious to inconspicuous, of linear to narrowly triangular or oblong scales (Figs. 1D, I) or linear bristles (Fig. 1M), these usually 5–15(–30)% the length of the longest primary bristles; rarely up to 40% (some specimens of *H. mucronata* var. *harmsiana*), secondary inner bristles many (*H. oregona*, Fig. 1L) to few or absent (e.g., *H. villosa* var. *nana*), 35–85% the length of the longest primary bristles, sometimes grading in length from linear secondary outer bristles into the primary outer bristles (e.g., *H. brandegei*, *H. stenophylla*, *H. thiniicola*); primary inner bristles tapering distally, 85–95% the length of the primary inner bristles, fewer than the primary

TABLE 1. Pappus variation in subtribe Chrysopsidinae; disc floret cypselae (ray fruit for *B. hirtella*). **Clv**, degree of clavateness of primary inner bristles (0 = not clavate to 4 = strongly clavate); **Clv-Tap**, clavate alternating with tapered bristles (primary inner and outer whorls, y = yes, - not obviously so); **Lgth**, primary outer bristles shorter than primary inner bristles; **Ovrlp**, degree of overlapping of bristles at the base (0 = not observed; 1 = slight overlap; 2 = definite overlap); **2nd-O**, evidence for a secondary outer whorl of short scaly-bristles; **2nd-O wid**, width of the secondary outer bristles (0 = linear, 1 = narrowly triangular, 2 = lanceolate); % = length compared to 1° inner bristles; **No. Br** = approximate number of mid to long bristles (2nd inner, 1° outer and inner whorls; small sample size); percents listed are bristle lengths compared to the length of the primary inner series.

Taxon Clv	Clv-Tap	Lgth	Ovrlp	2nd-O	2nd-O wid	2nd-O %	No. Br	Comments
***Heterotheca* (*x*=9)**								
sect. *Heterotheca* (dimorphic; ray cypselae nearly always lack pappus)								
H. grandiflora	1	y	y	1	y	0–1	5–15%	50–60	2nd inner bristles few, 40–70%
H. inuloides								
var. *inuloides*	1–2	y	y	1	y	1	5–15%	60–65	2nd inner bristles many, 35–65%
var. *roseum*	1	y	y	1	y	0–1	5–10%	60–65	2nd inner bristles few, 50–70%
var. *viridis*	0–1	y	y	1	y	1	5–10%	60–65	2nd inner bristles few, 70–80%
H. leptoglossa	2	y	y	1	y	1	5–15%	35–45	2nd inner bristles few, 70–80% grading into 1° outer bristles
H. subaxillaris								
subsp. *latifolia*	1	y	y	2	y	0–1	5–10%	25–30	2nd outer bristles 5–10%; 2nd inner bristles 0–very few, 60–70%
subsp. *subaxillaris*	1	y	y	1	y	0–1	5–15%	30–45	2nd outer bristles 5–10%; 2nd inner bristles few, 40–70%
sect. *Ammodia* (rayless)								
H. oregona								
var. *compacta*	1	y	y	1	y	0	5–8%	60–75	2nd outer bristles obscure; 2nd inner bristles few, 50%
var. *oregona*	1	y	y	2	y	0	5–10%	75–85	2nd outer bristles obscure; 2nd inner bristles few, 50%

TABLE 1. cont.

Taxon	Clv Tap	Clv-	Lgth	Ovrlp 0	2nd- wid	2nd-0 %	2nd-0 Br	No.	Comments
var. *rudis*	1	y	y	1	y	0	5–10%	50–55	2nd outer bristles few; 2nd inner bristles few, 40–70%
var. *scaberrima*	1	y	y	1	y	0	15–30%	60–70	2nd inner bristles few, 40–70%, grade into 1° outer bristles
sect. *Phyllotheca*									
H. brandegei (rayless)	1	y	y	1	y	0–1	10–15%	35–55	2nd inner 70–80%, grade into 1° outer bristles
H. canescens	1	y	y	1	y	1	5–10%	25–40	2nd inner bristles few, 50–70%
H. camporum									
var. *camporum*	1	y	y	1	y	0–1	10–15%	30–45	2nd inner bristles 0–few, 70%
var. *glandulissimum*	2	y	y	1	y	0–1	5–10%	30–45	2nd inner bristles few, 50–70%
H. fulcrata									
var. *amplifolia*	0–1	y	y	1	y	0–1	10–15%	35–45	2nd inner bristles few, 55–75%
var. *arizonica*	1	y	y	1	y	0–1	10–20%	35–45	2nd inner bristles very few, 60–65%
var. *fulcrata*	0–1	y	y	1	y	1–1+	10–15%	25–45	2nd inner bristles 0–few, 70–80%
var. *senilis*	1	y	y	2	y	1	5–15%	28–45	2nd inner bristles few, 70–85%, grade into 1° outer bristles
H. gypsophila	1–2	y	y	1	y	0	5–10%	30–40	2nd inner bristles few, 70–85%, grade into 1° outer bristles
H. jonesii	1	y	y	2	y	1	5–15%	25–35	2nd inner bristles 0–few, 70%
H. marginata	0–1	y	y	1	y	0–1	10–15%	40–52	2nd inner bristles very few, 70–80%
H. mexicana	0–1	y	y	1	y	0–1	10–15%	40–60	2nd inner bristles few, 40–60%
H. monarchensis	1	y	y	1	y	1+	10–15%	25–40	2nd inner bristles 0–very few, 70%
H. mucronata									
var. *mucronata*	1	y	y	1	y	0–1	5–10%	35–50	2nd inner bristles few, 80–85%
var. *harmsiana*	1	y	y	1	y	0–1	10–40%	35–40	2nd outer bristles can be long; 2nd inner bristles few, 70–80%

TABLE 1. cont.

Taxon	Clv	Clv-	Lgth	Ovrlp	2nd-	2nd-O	2nd-O	No.	Comments
	Tap			O	wid	%	Br		
H. pumila	0	–	y	2	y	0	10–20%	35–45	2nd inner bristles very few, 75–80%
H. rutteri	0	–	y	1	y	0–1	20–25%	35–46	2nd inner bristles very few, 75–80%
H. sessiliflora									
subsp. *bolanderi*	1	y	y	1	y	1	5–15%	50–70	2nd inner bristles few–many, 55–85%
subsp. *echioides*									
var. bolanderioides	2	y	y	1	y	1	x–x%	35–60	2nd inner bristles few, 55–70%
var. *echioides*	1	y	y	1	y	1	5–15%	25–50	2nd inner bristles 0 or few–many, 60–70%, some fruits have significantly few bristles and lack 2nd inner whorl
var. *camphorata*	2	y	y	1	y	1	5–15%	35–45	2nd inner bristles few, 60–70%
subsp. *fastigiata*									
var. *fastigiata*	0–1	y	y	2	y	0	5–30%	50–70	2nd inner bristles many, 45–85%, grade into 2nd outer and 1° outer whorls
var. *sanjacintensis*	1	y	y	2	y	0	5–30%	50–80	2nd inner bristles many, 45–85%, grade into 2nd outer and 1° inner whorls
subsp. *sessiliflora*	1–2	y	y	2	y	1+	5–10%	45–50	2nd inner bristles few, 50–70%
H. shevockii	1	y	y	0	y	0–1+	5–10%	35–45	2nd inner bristles few, 60–65%
H. stenophylla									
var. *angustifolia*	1	y	y	1	y	0–1	5–15%	35–45	2nd inner bristles few, 50–70%, grade into 1° inner bristles
var. *stenophylla*	1	y	y	1	y	0	15–10%	25–42	2nd inner bristles few, 60–70%, grade into 1° inner bristles
H. thiniicola	1	y	y	2	y	0	10–25%	25–35	2nd inner bristles many, 30–60%, grade into 2nd outer and 1° inner

TABLE 1. cont.

Taxon	Clv Tap	Clv-	Lgth	Ovrlp 0	2nd- wid	2nd-0 %	2nd-0 Br	No.	Comments
H. villosa									
var. *ballardii*	1	y	y	1	y	0–1	5–10%	35–45	2nd inner bristles few, 60–70%%
var. *depressa*	1	y	y	1	y	0	10–15%	35–45	2nd inner bristles few, 50–65%
var. *foliosa*	1–2	y	y	0	y	0–1	8–15%	35–45	2nd inner bristles few, 60–65%
var. *minor*	1	y	y	2	y	0–1	5–15%	30–45	2nd inner bristles few, 60–70%
var. *nana*	1–2	y	y	0	y	0–1	10–15%	28–40	2nd inner bristles 0–very few, 65%
var. *pedunculata*	2	y	y	1	y	1	10–25%	25–45	2nd inner bristles 0–very few, 80%
var. *scabra*	1	y	y	0	y	0–1	8–15%	35–45	2nd inner bristles very few, 60–70%, grade into 1° inner bristles
var. *sierrablancensis*	1–2	y	y	1	y	0–1	10–15%	35–45	2nd inner bristles 70–80%, grade into 1° inner bristles
var. *villosa*	1	y	y	0	y	0	5–15	30–50	2nd inner bristles 60–70%, grade into 1° inner bristles
H. viscida	1–2	y	y	0	y	1	5–15%	23–40	2nd inner bristles very few, 50–60%
H. zionensis	1	y	y	1	y	0	10–15%	30–45	2nd inner bristles few, 50%
Noticastrum (*x*=9)									
N. acuminatum	0–1	y	y	2	y	0	5–20%	75–90	2nd inner bristles many, 65–75%
N. calvatum	0–1	y	y	2	y	0	5–10%	90–100	2nd inner bristles few, 80%
N. diffusum	0–1	y	y	2	y	0	10–30%	75–80	barbs of bristles tinted red; 2nd inner bristles few, 60–80%
N. gnaphaloides	0–1	y	y	2	y	0	5–10%	100–115	2nd inner bristles few, 80%
N. hatsbachii	0–1	y	y	2	y	0	10–20%	45–50	2nd inner bristles few, 40–80%
N. macrocephalum	0–1	y	y	2	y	0	10–30%	80–90	2nd inner bristles few, 80–85%
N. marginatum	1	y	y	2	y	0	5–15%	75–80	2nd inner bristles few, 70–85%
N. sericeum	0–1	y	y	2	y	0	10–20%	120–125	2nd inner bristles few, 70–80%

TABLE 1. cont.

Taxon	Clv Tap	Clv-	Lgth	Ovrlp 0	2nd- wid	2nd-0 %	2nd-0 Br	No.	Comments
***Tomentaurum* (unknown)**									
T. nivea	0–1	y	y	2	y	0	10–20%	75–85	2nd inner bristles few to many, 60–70%
Pityopsis (*x*=9)									
sect. *Pityopsis*									
P. falcata	0–1	y	y	1	y	0	10–15%	30–40	2nd inner bristles 0–few, 45–80%
P. flexuosa	1	y	y	1	y	0	5–10%	30–50	2nd inner bristles 0–few, 45–85%
P. pinifolia	1	y	y	2	y	1	10–15%	25–30	2nd inner bristles not seen
P. ruthii	0–1	y	y	1	y	1	5–15%	25–35	2nd inner bristles, few, 40–85%
sect. *Graminifoliae*									
P. aspera									
var. *adenolepis*	0–1	y	y	2	y	0–1	10–20%	25–35	2nd inner bristles 0–few, 70–80%
var. *aspera*	0–1	y	y	1	y	0–1	5–15%	30–35	2nd inner bristles few, 70–80%
P. graminifolia									
var. *aequilifolia*	0	y	y	0	y	0–1	10–15%	40–45	2nd inner bristles 0–few, 70–80%
var. *graminifolia*	1	y	y	2	y	0	10–20%	32–40	2nd inner bristles few, 75–85%
var. *latifolia*	0	y	y	1	y	0	5–15%	35–45	2nd inner bristles 0–few, 60–85%
var. *tenuifolia*	0	y	y	1	y	0–1	5–15%	35–45	2nd inner bristles 0–very few, 70–85%, grading into 1° outer bristles
var. *tracyi*	0–1	y	y	0	y	0–1	5–10%	35–45	2nd inner bristles few, 50–85%
P. oligantha	0–1	–	y	1	y	0–1	5–10%	25–40	2nd inner bristles 0–very few, 75–85%
***Croptilon* (*x*=7,6,5,4)**									
C. hookerianum									
var. *graniticum* (*x*=7)	0	–	y	0	y	0	5–20%	30–35	2nd whorls absent or very rarely a short linear bristle present

TABLE 1. cont.

Taxon	Clv Tap	Clv-	Lgth	Ovrlp 0	2nd- wid	2nd-0 %	2nd-0 Br	No.	Comments
var. *hookeri* (*x*=6)	0	–	y	0	y	0	5–10%	25–30	2nd outer bristles 0–few; 2nd inner bristles 0–few, 50–70%
var. *validum* (*x*=5)	0	–	y	0	y	0	(5–10%)	25–30	2nd outer bristles 0–very rarely vestigial (or abnormal short 1° bristle)
C. rigidifolium (*x*=6, 5)	0	–	y	0	n	0	5–10%	25–30	2nd out bristles 0–few; 2nd outer bristles few 35–75%, grade into 1° bristles
C. divaricatum (*x*=4)	0	–	y	1	n	–	–	25–30	2nd outer bristles not seen; 1° outer bristles 70–80%, sometimes grade into 1° inner
***Bradburia* (*x*=4,3)**									
B. hirtella	0–1(–2)	y	y	2	y	2	10–15%	30–36	ray florets—2nd inner bristles few, 50–60%; 1° outer 70–95%, grade into 1° inner; see text for comments on pigmentation: disc florets—reduced pappus, 0–5 short scales to long broad-based bristles
B. pilosa	0(–1)	y	y	0	y	2	8–20%	18–25	2nd outer whorl of large, obvious to naked eye, lanceolate–oblong scales 0.1–0.2 mm wide; 2nd inner bristles 0–few, 75–85%, usually absent, grade into 1° bristles; 1° outer bristles few, grade into 1° inner bristles; see text for comments on pigmentation.

TABLE 1. cont.

Taxon	Clv	Clv-	Lgth	Ovrlp	2nd-	2nd-O	2nd-O	No.	Comments
	Tap			O	wid	%	Br		
***Chrysopsis* (*x*=5, 4 and x_2 = 9; most species lack 2nd inner bristles and have few primary outer bristles)**									
C. delaneyi	2	y	y	0	y	0	15–25%	30–40	2nd inner bristles not seen
C. floridana	1	y	y	1	y	0	10–15%	25–30	2nd inner bristles not seen
C. godfreyi									
var. *godfreyi*	2	y	y	0	y	0	10%	30–35	2nd inner bristles not seen
var. *viridis*	1	y	y	–	y	0	5–10%	30–35	2nd inner bristles not seen
C. gossypina (x_2 = 9)									
subsp. *cruiseana*	1	y	y	0	y	0–1	10–15%	30–35	2nd inner bristles not seen
subsp. *gossypina*	1	y	y	0	y	0–1	10–15%	25–35	2nd inner bristles not seen
subsp. *hyssopifolia*	1	y	y	0	y	0–1	10–15%	25–30	2nd inner bristles not seen
C. highlandsensis	2–3	y	y	1	y	0	10–25%	30–35	2nd inner bristles very few, 55–60%
C. lanuginosa	2	y	y	0	y	1	10–15%	25–30	2nd inner bristles not seen
C. latisquamea	1	y	y	1	y	0	10–15%	30–35	2nd inner bristles not seen
C. linearifolia									
subsp. *dressii*	2	y	y	–	y	1	5–15%	20–35	2nd inner bristles not seen
subsp. *linearifolia*	2	y	y	–	y	0–1	10–15%	25–30	2nd inner bristles not seen
C. mariana (*x* = 4)	1–2	y	y	1	y	0–1	5–15%	25–30	2nd outer bristles no wider than in some other species of genus (sample includes 2*x*, 4*x*, 6*x*, 8*x*); 2nd outer bristles absent; 1° outer bristles 0–few
C. scabrella	2	y	y	1	y	0	15–30%	25–35	2nd inner bristles not seen
C. subulata	2	y	y	2	y	0–1	8–15%	20–25	2nd inner bristles not seen
***Osbertia* (*x*=5)**									
O. bartlettii	0	–	y	0	n	–	–	20–25	1° vary in length (80–100%); one fruit had 1 fine 2nd bristle 25% the

TABLE 1. cont.

Taxon	Clv Tap	Clv-	Lgth	Ovrlp 0	2nd- wid	2nd-O %	2nd-O Br	No.	Comments
O. chihuahuana	1–2	y	y	0–1	y	0	5–12%	25–30	length of the longest 1° bristles 2nd outer bristles few; 2nd inner bristles 45–65% of the length of the longest 1° bristles; 1° outer bristles 85–95%, grade into 1° inner bristles
O. stolonifera	0–1	–	y	1	y	0	5–40%	25–30	2nd outer bristles grade into 2nd inner bristles; 2nd inner bristles 50–70% of the length of the longest 1° bristles; 1° outer bristles 90–95%, grade into weakly clavate 1° inner bristles

inner bristles; primary inner bristles very weakly (Fig. 1B) to moderately clavate (Fig. 1K), 3.4–10 mm long.

***Noticastrum* (x = 9; eight of 19 species examined).**—Cypselae straw colored to brown, fusiform, 4–6 mm long, sparsely to moderately strigose, sometimes stipitate glandular distally (Fig. 2B–C) or over entire surface (Fig. 2H); ribs, 16–22, surface between ribs usually golden-brown, translucent, resin filled; pappi quadruple, each series usually grading into next, 45–125 mid to long bristles, averaging about 87 per fruit for the genus, straw colored, orange-rust or purplish (e.g., *N. diffusum*; Fig. 2A), yellow-rust pigment in shaft over entire length, the red pigment concentrated in the barb tips (Fig. 2F), barbs evenly arranged around the round shaft along the entire length of the bristles; secondary outer series obvious to inconspicuous, linear triangular scales (Figs. 2N) to linear bristles (Fig. 2B), usually 5–20(–30)% the length of the longest primary bristles; secondary inner bristles many, 40–85% the length of the longest primary bristles (Fig. 2E); primary inner bristles many, 85–95% the length of the primary inner bristles; primary inner bristles very weakly (Fig. 2D) to sometimes moderately clavate, 7–14 mm long, much exceeding the disc corolla lobes.

***Tomentaurum* (x = unknown; monotypic, *T. nivea* examined).**—Cypselae fusiform, 4–5 mm long, densely strigose (Figs. 3B–C); ribs 10–18, shallow, obscured by hairs; pappi quadruple, each series usually grading into next, 75–85 mid to long bristles, averaging about 80 per fruit, straw colored, barbs evenly arranged around the round shaft along the entire length of the bristles; secondary outer series obvious to inconspicuous, very linear triangular scales to tapering bristles (Figs. 3H–I), 10–20% the length of the primary inner bristles; secondary inner bristles few to many, 40–85% the length of the longest primary bristles (Fig. 3G); primary inner bristles many, 85–95% the length of the primary inner bristles (Fig. 3D); primary inner bristles very weakly to weakly clavate (Fig. 3E–F), 10–11 mm long.

***Pityopsis* (x = 9; all seven species, all 11 taxa examined).**—Cypselae straw colored to often dark reddish-brown, narrowly to broadly fusiform, 3–4 mm long, ribs 8–10, sparsely to moderately densely strigose; pappi quadruple or sometimes triple through loss of the secondary inner series, 25–46 mid to long bristles, averaging about 37 per fruit for the genus, light tan to straw colored, sometime pale rust colored proximally, barbs evenly arranged around the round shaft along the entire length of the bristles; secondary outer series of linear (Figs. 4E, G arrows) to broad (Figs. 4K–L), barbed scales, 5–15(–20)% the length of the primary inner bristles; secondary inner series of tapering bristles, few, 45–85% the length of primary inner bristles; primary outer series of tapering bristles 90–95% of primary inner bristles (Figs. 4C–D, F, H; arrows); primary inner series of weakly clavate bristles (Fig. 4D), 4–9 mm long.

***Croptilon* (x = 7, 6, 5, 4; all three species, all five taxa examined).**—Cypselae straw colored to brown or reddish-brown, sometimes mottled, fusiform to nar-

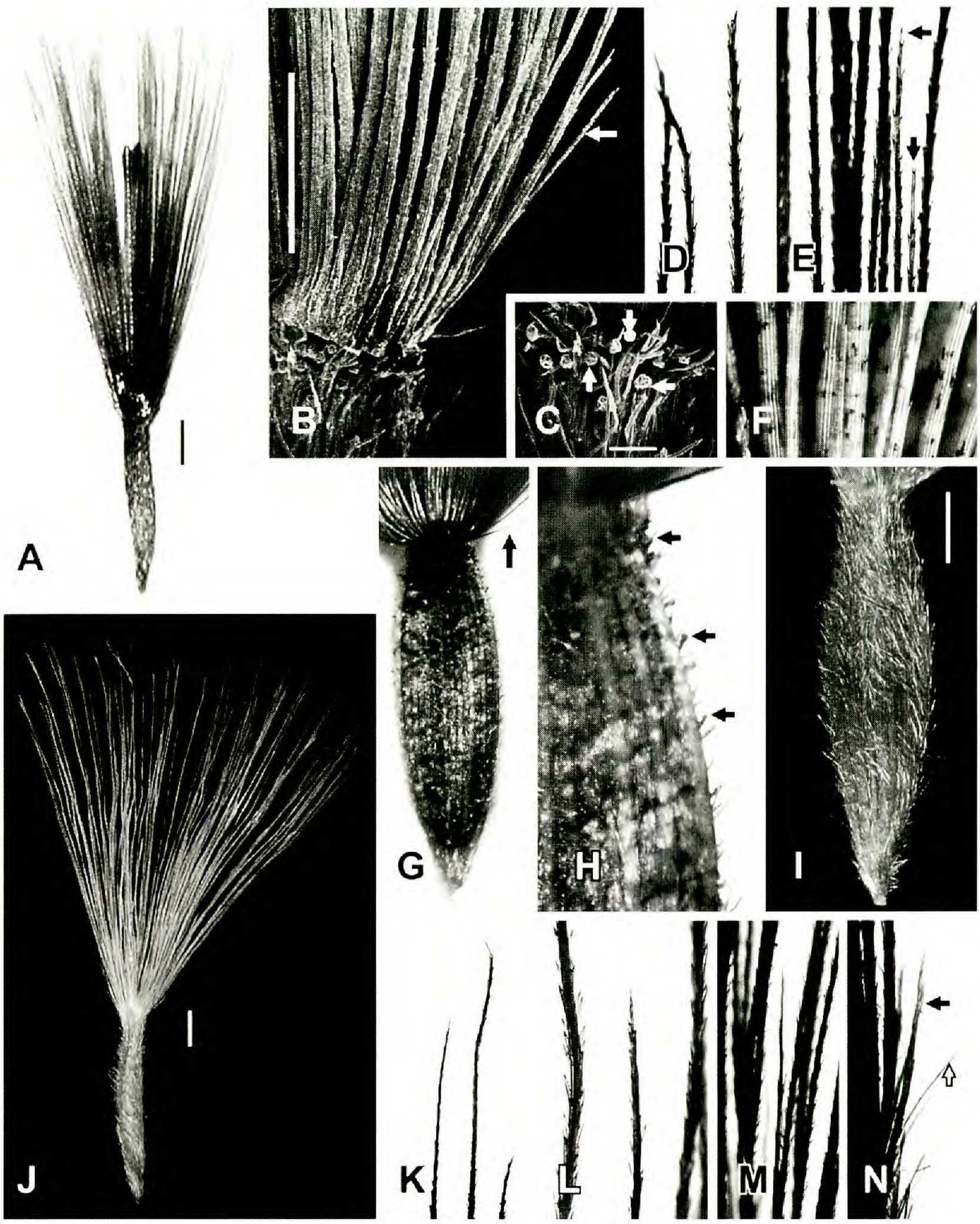

FIG. 2. Fruit and pappus traits of *Noticastrum*, disc fruits; scale bars = 1 mm (unless otherwise noted). **A–F.** *N. diffusum* (*Zardini 1094* TEX). **A.** Fruit with rusty reddish anthocyanotic quadruple pappus. **B.** SEM of mature fruit showing linear secondary outer bristles (arrow) and the bases longer series bristles; scale bar = 0.5 mm. **C.** SEM of stipitate glands (arrows) on upper fruit body; scale bar = 100 μm. **D.** Tips of primary inner series bristles. **E.** Tips of secondary inner series bristles (arrows) among much longer primary series bristles. **F.** Base of pappus bristles with anthocyanotic barbs. **G–H.** *N. calvatum* (*Hatschbach 52819* MO). **H.** Fruit body and secondary outer pappus bristle (arrow). **I.** Detail of multi-ribbed fruit body with stipitate glands (arrows). **I–J.** *N. macrocephalum* (*Montes 14942* MO). **I.** Mature fruit body. **J.** Immature fruit with four series of bristles. K. Tips of non-clavate to very weakly clavate primary bristles. **L.** Tip of primary outer bristle and near-tip portion of a longer primary bristle. **M.** Tip of secondary inner bristle and upper mid portions of much longer primary series bristles. **N.** Short secondary outer pappus bristle (solid arrow) and long hair of fruit body (open arrow).

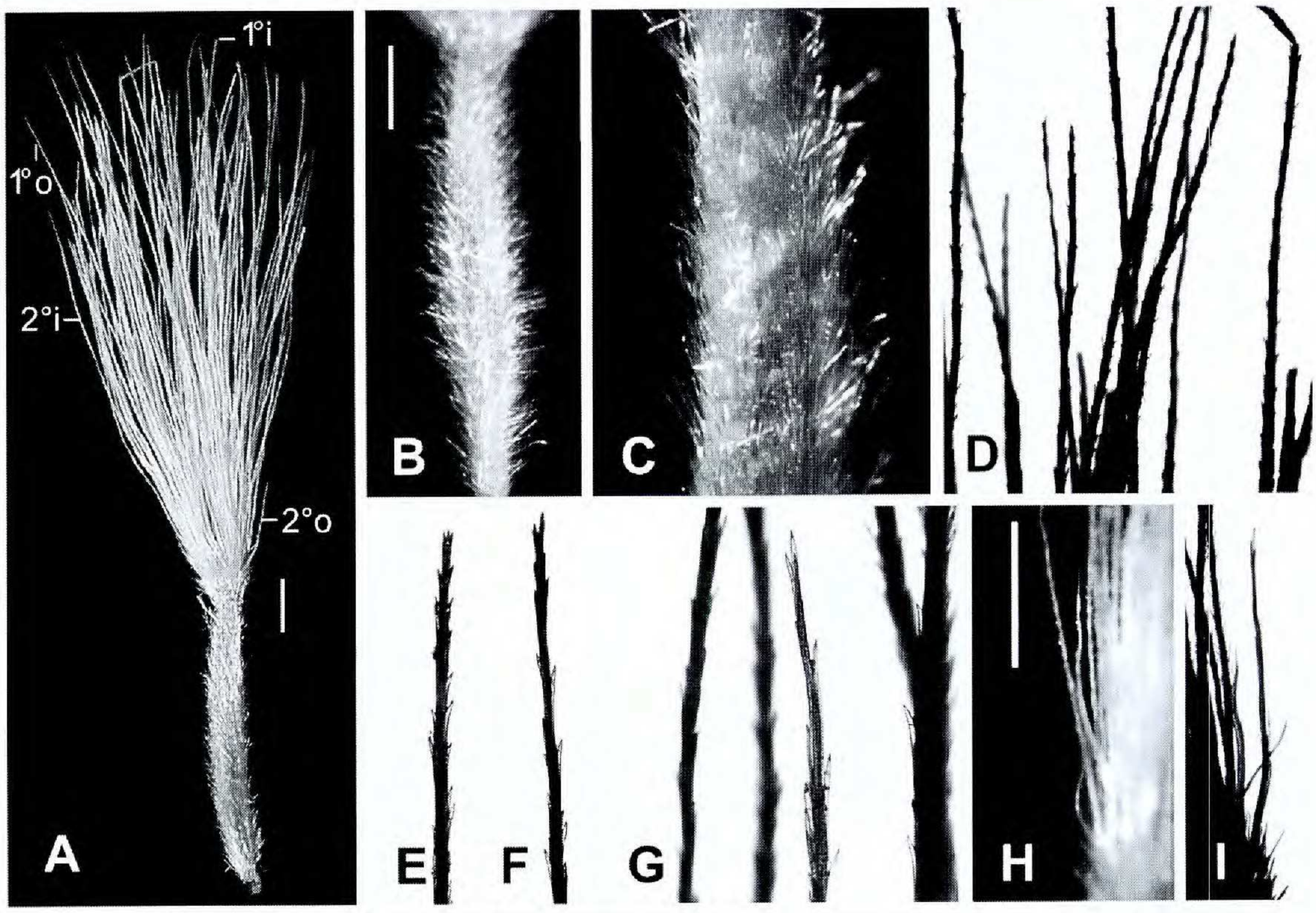

FIG. 3. Fruit and pappus traits of *Tomentaurum nivea*, disc fruits (*Pringle 1645* MO); scale bars = 1 mm in A–B, = 0.5 mm in H. **A.** Nearly mature fruit with secondary outer series (1°o), secondary inner series (2°i), primary outer series (1°o) and primary inner series (1°i) bristles indicated. **B.** Fruit body. **C.** Mid portion of fruit body. **D.** Tips of long primary bristles, a few are broken off. **E–F.** Tips of primary inner bristles. **G.** Tip of secondary inner bristle (center) and mid portions of four primary bristles. **H–I.** Secondary outer series bristles.

rowly obconic, 2–3.2 mm long, ribs 10–20, sometimes either the ribs or faces between them golden-brown to brown translucent, resin filled, sparsely to moderately densely strigose (Figs. 4A, G, K); pappi quadruple, triple, double, or sometimes single, 25–35 mid to long bristles, averaging about 28 per fruit for the genus, somewhat to dark rust colored in shaft, darkest proximally, becoming paler to whitish distally, barbs not pigmented, barbs evenly arranged around the round shaft along the entire length of the bristles; secondary outer series of linear bristle-like scales, 0–few (Figs. 5D–E, I–J, N–O), 5–10(–20)% the length of the primary inner bristles (Figs. 5D–F, I–J, O); secondary inner series of tapering bristles, absent or rarely 1–2, 50–70% the length of primary inner bristles (Fig. 5A, M; arrow) or these just atypically short primary outer series bristles; primary outer series of tapering bristles 80–95% of primary inner bristles, grading into primary inner bristles (Figs. 5A, 5G, 5K–L); primary inner whorl of non-clavate/very weakly clavate (Fig. 5B) to weakly clavate bristles (Fig. 5L), 4–9 mm long.

Croptilon has been treated as *Haplopappus* sect. *Isopappus* (Hall 1928; Smith 1965) and described as having a pappus with "a single series of equal (or nearly

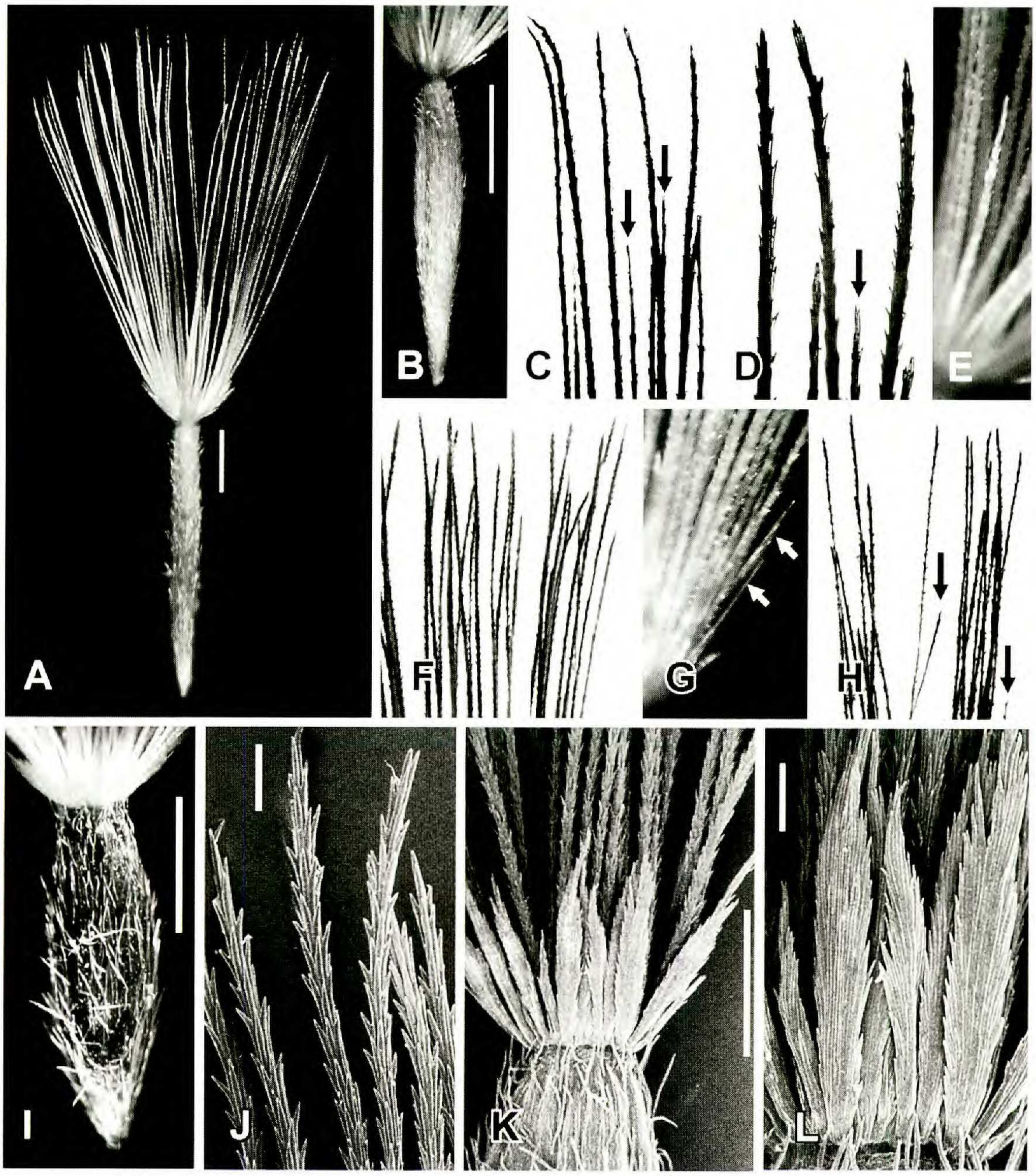

FIG. 4. Fruit and pappus traits of *Pityopsis*, disc fruits; scale bars = 1 mm in A–B and I, = 100 μm in J, = 0.5 mm in K, and = 0.1 mm in L. **A.** *P. graminifolia* var. *aequilifolia*, mature fruit (*Semple et al. 3992* WAT). **B–E.** *P. falcata* (*Semple 3366* WAT). **B.** Fruit body. **C–D.** Tips of weakly clavate primary inner bristles and attenuate, shorter primary outer bristles (arrows). **E.** Bristly secondary outer series linear scale. **F–G.** *P. flexuosa* (*Godfrey 75754* WAT). **F.** Tips of primary inner and outer bristles. **G.** Bristly secondary outer series scales (arrows) **H.** *P. pinifolia* (*Semple 10537* WAT, tips of primary inner and outer (arrows) series bristles. **I–L.** *P. aspera* var. *adenolepis* (*Semple et al. 4041* WAT). **I.** Mature fruit body. **J–L.** SEMs. **J.** Clavate tips of primary inner series bristles. **K–L.** Secondary outer series scales (differentially highlighted to clarify in K) and proximal portions primary series bristles.

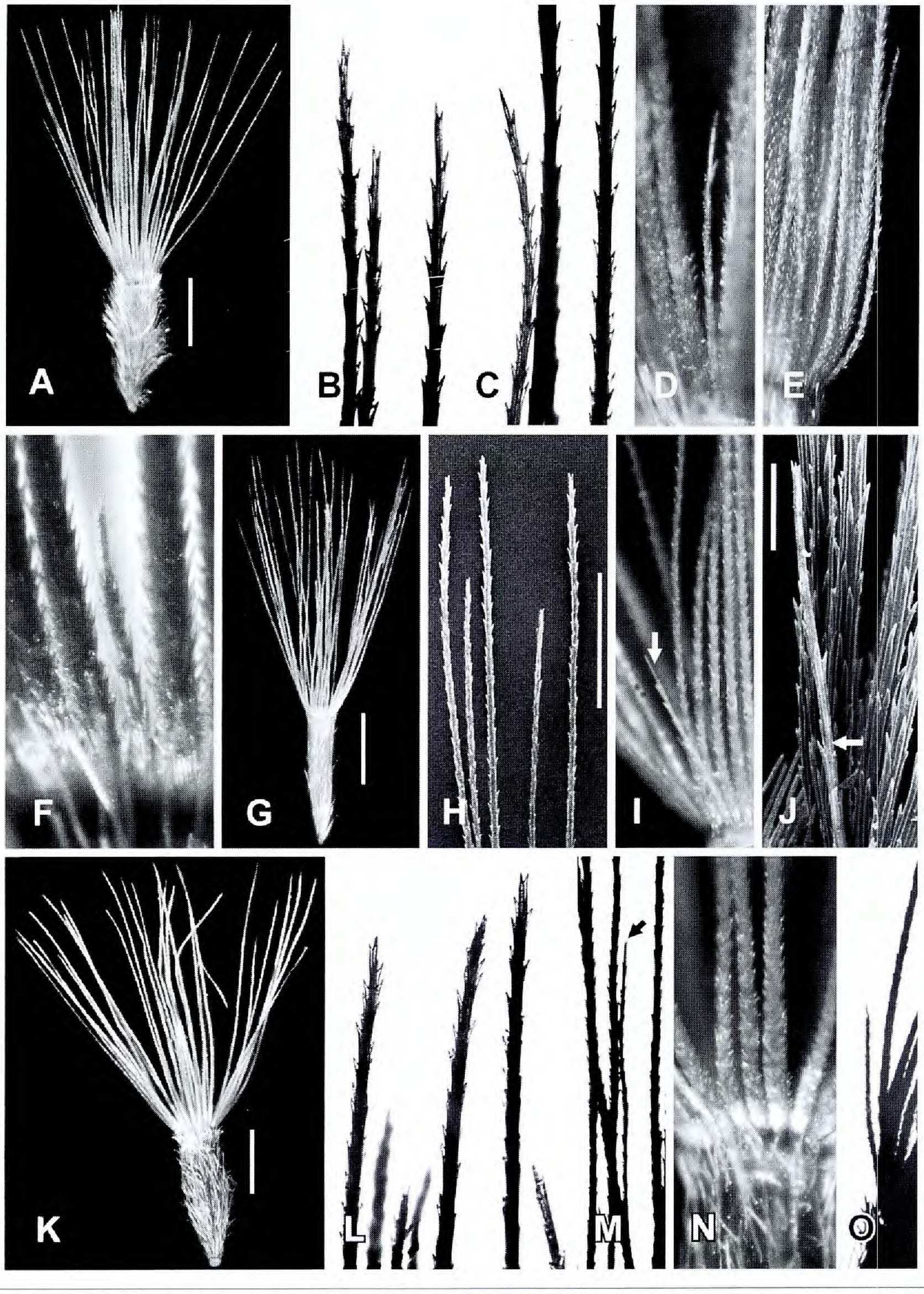

FIG. 5. Fruit and pappus traits of *Croptilon*, disc fruits; scale bars = 1 mm. **A–D.** *C. hookerianum* var. *hookerianum*. **A.** Mature fruit (*Semple & Brouillet 3363* WAT). **B–D.** *Turner et al. 46* TEX-LL. **B.** Tips of primary bristles. **C.** Tips of secondary inner bristle and upper mid portions of two longer bristles. **D.** Tip of secondary outer bristle. **E.** *C. hookerianum* var. *graniticum*, secondary outer bristle (E.B. *Smith 622* TEX). **F.** *C. hookerianum* var. *validum*, secondary outer bristle (*Rowell 4259* TEX). **G–J.** *C. rigidifolium* (G and I, *Cory 11886* TEX; H and J, *Nesom 5216* TEX, SEMs). **G.** Mature fruit. **H.** Tips of primary bristles. **I–J.** Bases of primary bristles and secondary outer bristles (arrows). **K–M.** *C. divaricatum* (*Semple & Chmielewski 6000* WAT). **K.** Mature fruit. **L.** Tips of primary bristles. **M.** Mid length secondary inner bristle (arrow) and mid portions of longer primary bristles. **N.** Bases of primary bristles. **O.** Short secondary outer linear bristle.

equal) capillary bristles, more or less ferruginous" (Smith 1965). Nesom (2000) as noted in the introduction also described the pappus as being in a single series. The results presented here indicate that the pappus neither consists of a single series nor are the bristles equal or nearly equal. The higher base number taxa (e.g., *C. hookerianum* var. *graniticum* with x=7) are more likely to have three or four series of bristles, while the lowest base number taxon, *C. divaricatum* with x = 4, may have only 1–2 series. The gradation in lengths of longer bristles and the lack of clearly clavate bristle tips results in uncertainty in determining the number of series present. The conclusion that multiple series are present is based on observations of many fruits, some of which have longer bristles of 2–3 distinct lengths. The much shorter outer bristles clearly exterior to the long bristles are essentially the same as the secondary outer series scales/bristles of some species of genera long recognized to have a short outer series, e.g. *Heterotheca*, *Noticastrum*, *Pityopsis* and *Chrysopsis*. The small fruit size generally correlates with a lower number of bristles and very few bristles in some series.

***Bradburia* (x = 4, 3; two species with very different pappi traits).**—1) *B. hirtella*: ray florets fertile, disc florets functionally staminate, ovary aborts; ray floret cypselae straw colored to brown or reddish-brown, obconic, ± triangular in cross-section, ca. 2 mm long, 5–10 shallow ribs per face, moderately strigose, more densely so along angles (Fig. 6A); pappi quadruple or triple, the series grading into each other, 18–26 mid to long, long-barbellate bristles (Fig. 6A), densely pigmented red proximally to only the barbs pigmented one third to one half the length, pale yellow to pale rust grading to white distally; secondary outer bristles linear, 5–20% the length of the longest inner bristles (Fig. 6B), barbs evenly arranged around the round shaft along the entire length of the bristles, uneven on the distal portion of the longer bristles; secondary inner bristles grading from secondary outer into primary outer, tapering, 25–85% the length of primary inner bristles; primary inner bristles round proximally, flattened distally and weakly to moderately clavate (Fig. 6C), 2.5–3.5 mm; mid to longer bristles pigmented proximally, the red pigment concentrated in the barbs (Figs. 6B, D). Disc floret pappi reduced to 0–5 scales and/or broad-based proximally flattened bristles (Figs. 6G–J), the longest weakly clavate (Fig. 6H). — 2) *B. pilosa*: ray and disc pappi similar, cypselae obconic, slightly compressed, sparsely strigose, 10–20 shallow ribs; pappi triple or double (Fig. 7K); secondary outer scales linear to lanceolate or oblong (Fig. 6L), 0.05–0.2 mm wide, barbellate proximally, margins jagged, especially distally; secondary outer bristles absent; primary outer bristles tapering, 0–2, 75–85% the length of the inner bristles; primary inner bristles tapering or only very remotely clavate; all longer bristles pigmented proximally with the concentration decreasing distally, yellow to rust, pigment in shaft, not barbs.

The combination of broad, whitish, light-reflecting scales and proximally

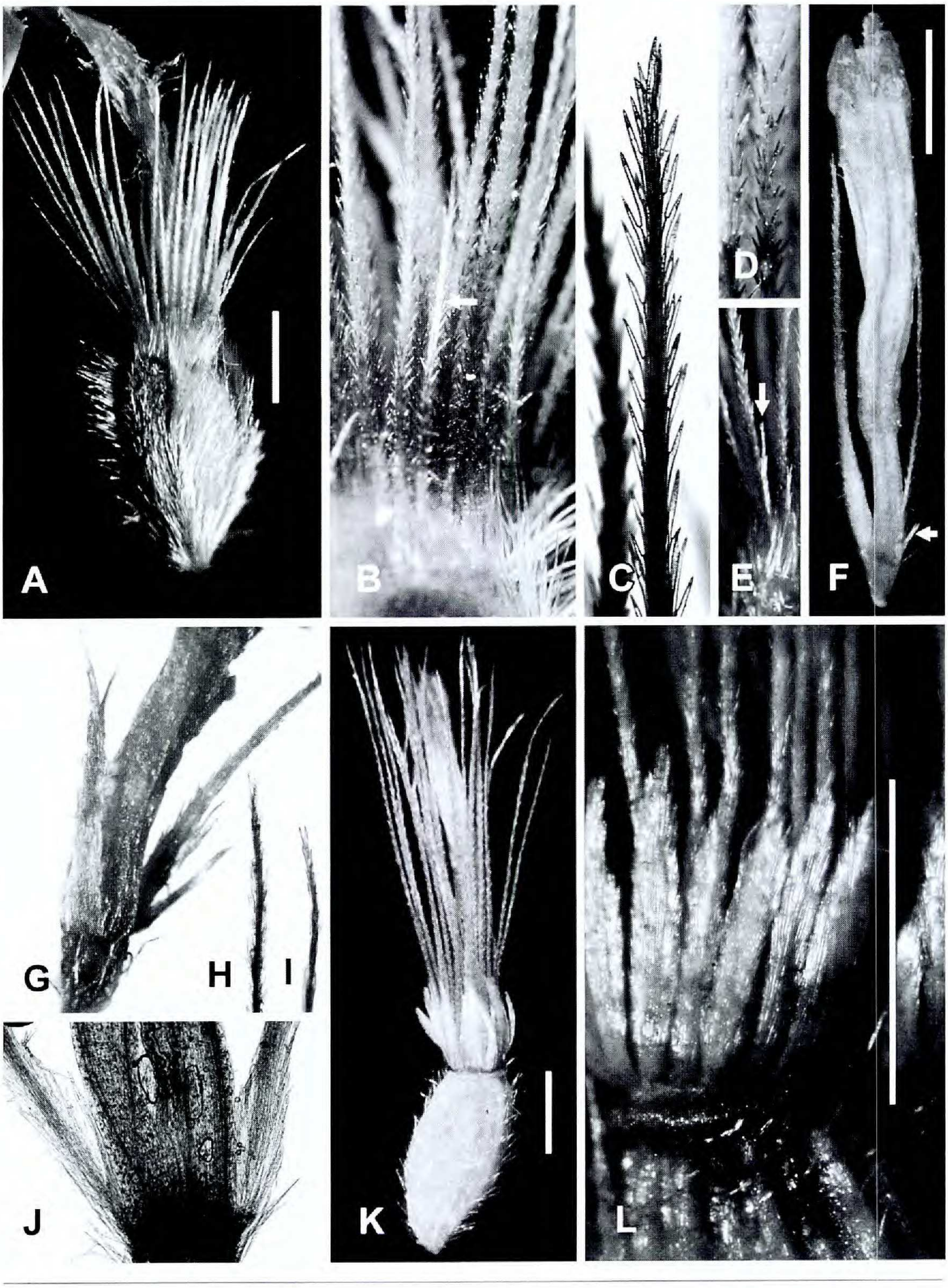

FIG. 6. Fruit and pappus traits of *Bradburia*; scale bars = 1 mm. A–J. *B. hirtella* (*Nesom 7470* WAT). **A–E.** Ray fruit. **B.** Pigmented terete bases of long bristles and long secondary outer bristle (arrow). **C.** Tip of distally flattened long primary inner bristle. **D.** Mid portion of bristles with distal barbs less pigmented then proximal barbs. **E.** Very small secondary outer bristle. **F–J.** Functionally staminate disc floret. **F.** Floret with one secondary outer scale (arrow) and two long broad-based bristles. **G.** Base of floret with broad scales. **H.** Tip of longer scale on right in G. **I.** Tips of shorter scale on left in G. **J.** Details of scales bases. **K–L.** *B. pilosa*, disc fruit (*Semple & Brammall 2753* WAT). **K.** Mature fruit. **L.** Secondary outer series scales.

darker-pigmented, long bristles as background makes the secondary outer series of *Bradburia pilosa* obvious to the naked eye. The narrower to mid-width scales are similar to broader scales in some species of *Chrysopsis* and *Heterotheca*. The widths of the secondary outer scales/bristles in *Heterotheca* and *Chrysopsis* form a continuum that overlaps at the wide end with the narrower width scales of *B. pilosa*. The broader scales of *B. pilosa* are unique in the subtribe. The broad scaly bases of the few, long bristles attached to the aborted ovary of the disc florets of *B. hirtella* are also unique in the subtribe. Possibly, the genes controlling normal scale and bristle development have been expressed together in single structures rather than separately in different series of structures in disc floret pappus development. Therefore, but in different ways, the two species of *Bradburia* have broader pappi members than found in all other genera in the subtribe.

The phylogenetic position of *Bradburia* is uncertain. Nesom (1991a, d) included the two species of *Bradburia* in *Chrysopsis* sect. *Bradburia*. Semple (1996) transferred *C. pilosa* to *Bradburia* as defined here. In the cladistic study by Semple and Tebby (1999), *Bradburia* grouped with *Croptilon* and *Heterotheca*, while *Chrysopsis* grouped with *Pityopsis*, *Noticastrum*, and *Tomentaurum*. Based on pappus traits, *Bradburia* is no more similar to *Croptilon* than to *Chrysopsis*. Pigmentation of bristles is similar in *Bradburia* and *Croptilon*, but a well developed secondary outer series is shared by *Bradburia* and *Chrysopsis*, although the scales are much broader on average in *B. pilosa* than in any species of *Chrysopsis*. A DNA sequence based phylogeny of the subtribe has not been published. Until such a study is completed, the phylogenetic position of *Bradburia* within the subtribe remains uncertain, although it is likely derived from either the *Croptilon* or *Chrysopsis* lineages, unless a separate dysploid series from $x = 9$ is hypothesized.

***Chrysopsis* ($x = 5, 4, x2 = 9$; all taxa examined, 11 species, 15 taxa).**—Cypselae straw colored or rarely dark red-purple, compressed obconic, smooth (Fig. 7G) or with 1–10 shallow ribs and sometimes 1–5, yellow to red brown, clavate, translucent ridges per side (Fig. 7D), sparsely to densely strigose, 1.5–3 mm; pappi triple or rarely quadruple, sometimes double in *C. mariana*, barbs evenly arranged around the round shaft along the entire length of the bristles; secondary outer series of linear (Fig. 7F) to narrowly triangular, jagged-edged scales (Figs. 7C, 7L), 0.4–1.4 mm, 5–15(25)% the length of the primary inner bristles, 20–40 mid to long barbellate bristles in 1–2(–3) series, whitish to straw colored; secondary inner series usually absent, rarely 1–3 tapering bristles 45–85% the length of primary inner bristles; primary outer series of tapering bristles 85–95% of primary inner bristles (Figs. 7B, E, I arrow, K); primary inner series of weakly to moderately clavate bristles (Figs. 7E, I–J), 4–7 mm long.

Some fruits of *C. mariana* ($x = 4$) have a true double pappus of just short secondary outer series scales and long, clavate primary inner series bristles (Fig.

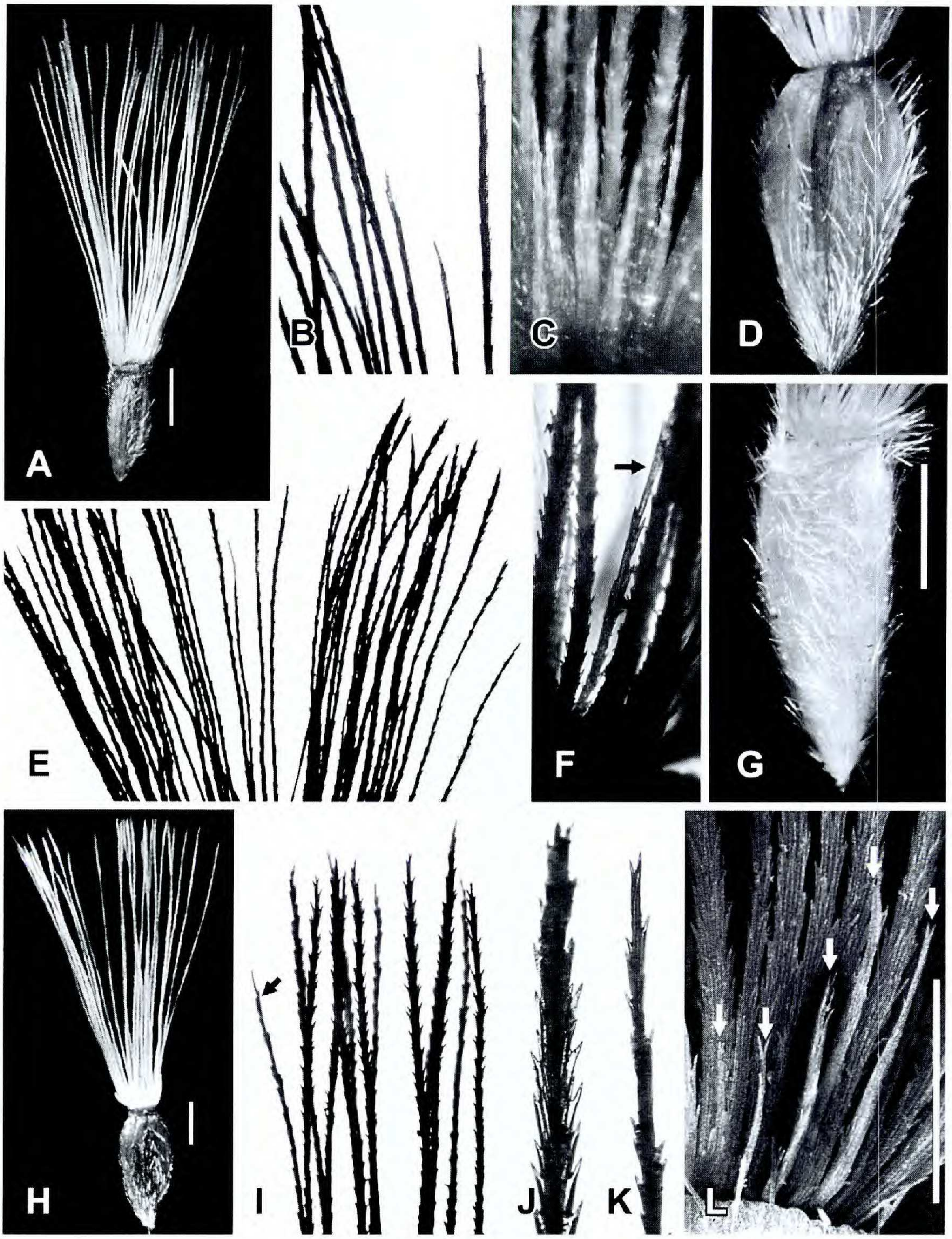

FIG. 7. Fruits and pappus traits of *Chrysopsis*, disc fruits; scale bars = 1 mm in A, G, and H; = 0.5 mm in L. **A–C.** *C. latisquamea* (*Semple et al. 2753* WAT). **A.** Mature fruit. **B.** Tips of primary bristles. **C.** Secondary outer bristle-like scales. **D.** Fruit body with enlarged translucent reddish-brown resin-filled rib, *C. gossypina* (*Semple et al. 3126* WAT). **E.** Distal portion of pappus, *C. delaneyi* (*Semple & Semple 7476* WAT). **F.** Linear secondary outer bristle-like scale (arrow); *C. linearifolia* (*Godfrey 75759* WAT). **G.** Mature fruit body, *Chrysopsis godfreyi* (*Semple & Godfrey 3149* WAT). **H–L.** *C. mariana* (*Semple & Chmielewski 6214* WAT). **H.** Mature purplish-red fruit with long primary inner series and short secondary outer series; 0–2 primary outer bristles on other fruits examined. **I.** Tips of primary inner bristles and one primary outer bristle (arrow). **J.** Linear to narrowly triangular secondary outer scales (arrows).

7H, 7L); others fruits produced by the same individual have a few tapering primary outer bristles (Fig. 7I). This is true for fruits at all four ploidy levels (2n=8, 16, 24, 32; Semple & Chinnappa 1986). In his cladistic study, Nesom (1991a) scored the secondary outer scales of both *Bradburia pilosa* and *C. mariana* as "(1) scales", but the latter has scales that are very narrowly triangular to only narrowly triangular on the same fruit like some other species of *Chrysopsis*, not like those of *B. pilosa*.

Osbertia (*x* = 5; three of three species examined) — Cypselae straw-colored to brown, cylindrical-fusiform, 1.0–1.5 mm long, sparsely strigose, ribs 8–16, superficial (Figs. 8N, T), sometimes either the ribs or faces between them golden-brown to brown translucent; pappi quadruple, triple, double (Fig. 8M) or single and rarely vestigially triple, the series distinct or grading into each other (Fig. 8A); 20–35 bristles, barbs evenly arranged around the round shaft along the entire length of the bristles, barbs sometimes small and less obvious; secondary outer bristles linear, 3–10, sometimes grading into secondary inner bristles, absent in *O. bartlettii* or very rarely one linear, fine, short bristle (Figs. 8R–S), 5–40% the length of the inner long bristles; secondary inner bristles tapering, fine, linear, 5–10, 45–70% the length of primary inner bristles, absent in *O. bartlettii*; primary outer bristles fewer than and often grading into the primary inner bristles, 85–95% the length of the primary inner; primary inner bristles weakly to sometimes moderately clavate tapering (Figs. 8C, I–J), or in *O. bartletii* tapering and subequal or the shortest 80% if all long bristles are included in a single series, 2.5–7.5 mm long.

The pappus of *Osbertia* differs in the three species, but in general all have rather linear and short-barbed bristles. The four series are most distinct lengthwise in *O. chihuahuana* (Figs. H–L) and least distinct or reduced to two or one series in *O. bartlettii*. In the type species *C. stolonifera*, the secondary outer and inner series grade together, as do the primary outer and inner series, but the secondary and primary series are clearly of different lengths (Figs. A–B). The two secondary outer series could be interpreted as a single series highly variable in length, and the primary outer and inner could be interpreted as a single series grading from non-clavate shorter bristles to weakly clavate longer bristles. Overall there is a spiral arrangement from very short, fine, outer bristles to long coarser inner bristles, with the outer members of the series clearly placed externally to and overlapping the longer inner members of the series.

Previous authors have considered the pappus of *Osbertia* to be simpler than described above. Turner and Sundberg (1986) described the pappus of *Osbertia* as having "numerous setae in a single series" 4–6 mm long. Nesom (2000) noted that *O. chihuahuana* Turner & Sundberg had "a short, outer series commonly present" (i.e., a double pappus) but did not describe the individual bristles or scales. Nesom (1991c) stated that pappus of *O. bartlettii* was "uniseriate, of 15–20 barbellate bristles without an outer series." The single short outer bristle

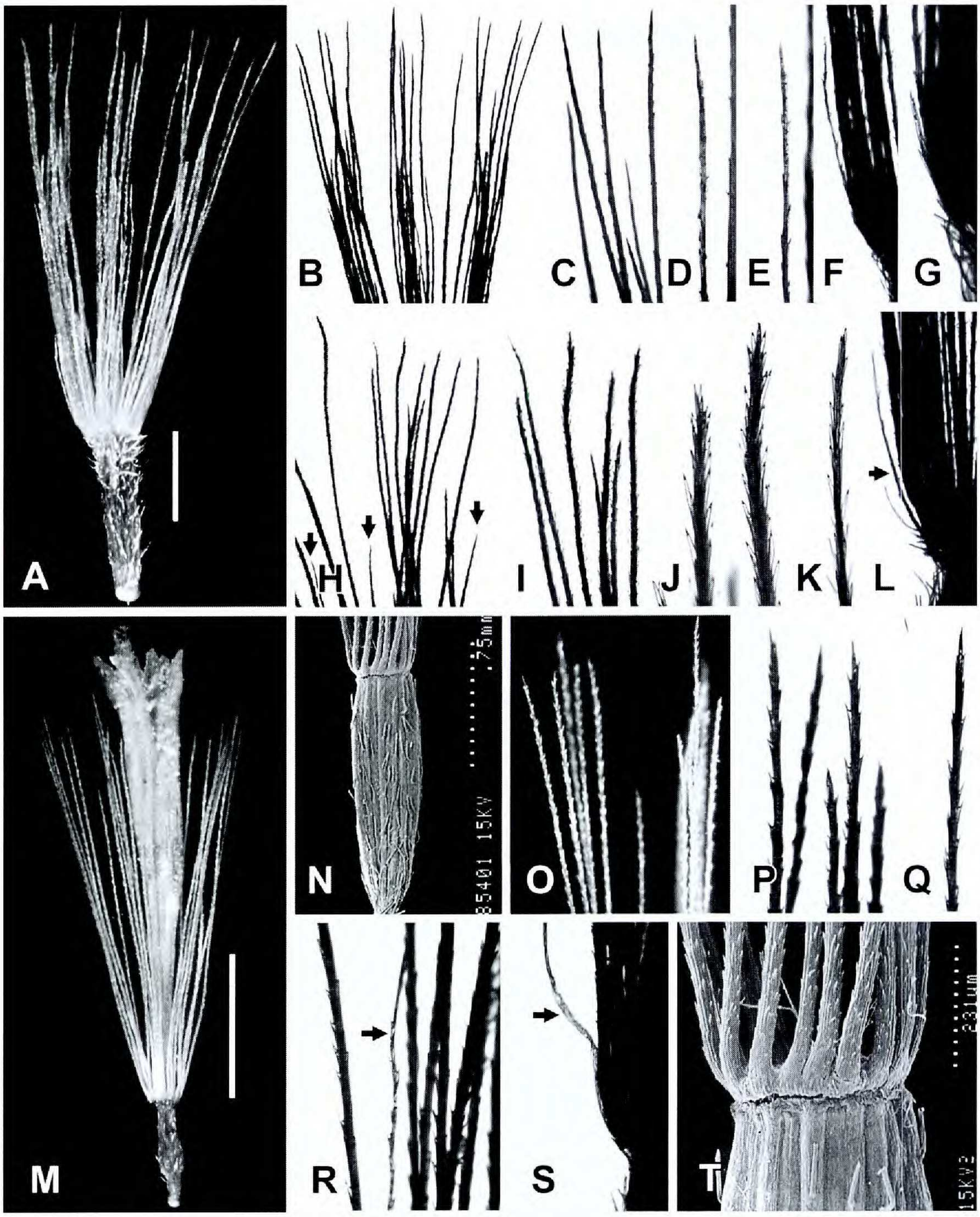

FIG. 8. Fruit and pappus traits in *Osbertia*, disc fruits; scale bar = 1 mm. **A–G.** *O. stolonifera* (*Ton 1027* TEX-LL). **A.** Immature fruit. **B.** Distal portion of longer bristles. **C.** Very weakly clavate primary inner bristles. **D–E.** Tips of mid length secondary outer bristles. **F–G.** Short and very short secondary outer bristles, respectively. **H–L.** *O. chihuahuana* (*Gonzales & Acevedo 2232* TEX). **H.** Distal half of pappus (arrows indicate possible secondary inner bristles). **I.** Distal portion of primary bristles. **J.** Tips of primary inner bristles. **K.** Tip of possible secondary inner bristles (center in H). **L.** Linear secondary outer bristle (arrow). **M–T.** *O. bartlettii* (*Nesom 6296* WAT; SEM images, *Muller 2854* UC. **M.** Immature fruit with disc corolla attached. **N.** Fruit body (SEM). **O–Q.** Tips of long primary bristles. **R–S.** Tip and base of rarely seen short outer bristle, respectively. **T.** Proximal portion of uniseriate pappus (SEM).

reported above was found on one fruit of the few present on the single collection of the species at WAT (*Nesom 6296*), but none were visible in the material from UC used for the SEM examination (Fig. 8H).

The phylogenetic position of *Osbertia* is uncertain and the genus only tentatively has been included here in the Chrysopsidinae. It was included in *Haplopappus* sensu lato by Hall (1928), which sensu stricto is part of the Machaerantherinae Nesom. Nesom (1991c) placed *Osbertia* in the Chrysopsidinae, and Nesom (2000) placed it close to *Chrysopsis*. In the RFLP DNA study by Lane et al. (1996), *Osbertia stolonifera* was placed basal to the clade including *Ericameria/Macronema*, *Xylothamia*, and *Tonestus* but was not included in the ITS DNA sequence study by Beck et al. (2004). In the latter study, *Ericameria*, *Xylothamia*, and *Tonestus* were each placed in different clades separate from the clade including *Heterotheca villosa* and *Chrysopsis gossypina*. The phylogenetic position of *Osbertia* within the North American clade needs additional study. On the basis of pappus traits, *Osbertia* fits into the subtribe Chrysopsidinae as a derived lower base number taxon with a reduced number of bristles, sometimes reduced number of series, and derived non-clavate to weakly clavate longer bristles. Further study is needed to determine if such traits would exclude it from other proposed subtribes.

SYSTEMATICS IMPLICATIONS

There is considerable variation in the pappi traits of taxa within the Chrysopsidinae, which can not be defined in part on the basis of usually having a double pappus. Even within individual genera there is variation in the number of series, how distinct the series are from each other, and the number of long bristles per fruit. There are patterns to the variation such that a "norm" for each genus can be given, but these are not diagnostic due to with-genus variation and overlapping of ranges of variation between genera. For example, the number of bristles in *Noticastrum*, with a quadruple pappus, is higher compared to other genera; the bristles in all series are linear; and the tips of the longest secondary inner bristles differ little from those of the shorter bristles in the primary outer series and secondary inner series. In *Heterotheca* with a usually quadruple pappus, the number of bristles averages less than *Noticastrum* but more than occur on the fruits of the lower base number taxa; and there are usually only a few mid-length bristles making up the secondary outer whorl. However, in *H. oregona* the number of bristles is within the range found in *Noticastrum*, but the series are generally discontinuous in length and thus do not grade into each other. In other species of *Heterotheca*, the bristle series grade into each other, but there are fewer bristles, e.g., *H. thiniicola*. In *Chrysopsis* with a usually triple pappus, the number of bristles and the absence of secondary inner bristles is fairly consistent; the primary inner bristles usually are more obviously clavate than in most species in other genera of the

subtribe; and fruits with relatively broad secondary outer scales have some linear scales. *Chrysopsis mariana* with $x = 4$ has a double pappus or "slightly" triple pappus (1–2 primary inner bristles), while the secondary outer scales are like other species in the genus and the primary inner bristles are obviously clavate (especially when examined at 50–100H). Although pappus descriptions of the genera of the Chrysopsidinae need to be longer to encompass the details and range of variation in the series of bristles, the individual genera themselves can not be diagnosed on the basis of pappus traits alone. Therefore, the details of pappus features presented here are likely to be more significant for cladistic/phylogenetic studies then for identifying specimens. The genera with the higher base numbers have more pappus elements in more series than do the lower base number genera with more derived and simpler pappi. Lastly, when the pappi of members of other subtribes have been examined in detail, general trends in differences of derived features may emerge. At this point, however, more data are needed.

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